# XV. *On the Development of the Parasitic Isopoda.*

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[Plates 45–47.]

The following paper contains an account of observations on the development of the species *Cymothoa œstroides* and *C. parallela* of Milne Edwards; but the forms of the young seem to show that several species are really included under these two names. In the early stages of development the only observable difference that exists between the embryos is one of size, but in the later stages they differ very markedly from each other in their external characters. From adult individuals answering the description of *C. œstroides* I have obtained four varieties of embryos: two with long antennæ and two with short.*

In the two former the first pair of antennæ are but slightly longer than the head, while the second pair are longer than the body; the eyes are small. In one of the varieties thus characterised the abdominal appendages are fringed with long hairs (fig. 20), and in the other they are smooth.

In the two latter both pairs of antennæ are short, and of about the same length, and the eyes are large. This group also contains one variety with smooth, and one with hairy abdominal appendages. From *C. parallela* I have obtained but a single form of embryo (fig. 21), which differs from the embryo of *C. œstroides* with short antennæ and smooth abdominal appendages only in being smaller, and not having so many pigment spots on the dorsal surface.

My work has been mainly carried on in the zoological station at Naples, and I take this opportunity of thanking Dr. Dohrn and Dr. Eisig for the kind way in which they have forwarded my researches. I have prepared the eggs in the way described by Bobretzky (Zeit. für Wiss. Zool., bd. xxiv.) in his paper "On the

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| * *C. œstroides* | I. Embryos with second pair of antennæ long. Eyes small . . . . . . . . . . . . . | 1. Abdominal appendages hairy. 2. Abdominal appendages smooth. |
| | II. Embryos with second pair of antennæ short. Eyes large . . . . . . . . . . . . | 3. Abdominal appendages hairy. 4. Abdominal appendages smooth. |

Development of *Oniscus Murarius*," namely, by heating them in water and then hardening them, first in bichromate of potash and then in alcohol, beginning with 70 per cent., and gradually increasing the strength to absolute. Some of the specimens were embedded in a mixture of solid paraffin and ordinary paraffin oil,* others in spermaceti and castor oil. In all cases the sections were stained with KLEINENBERG's hæmatoxylin and mounted in Canada balsam. I found that the most convenient way to heat the eggs was to put them in a test tube with a little sea water, and hold this in a vessel of boiling water for a few minutes.

The eggs are carried by the parent in a large brood-pouch until the young are able to swim as among the non-parasitic Isopoda. I have found both the adults† and young in all stages of development from the beginning of January to the end of June, so breeding probably continues all the year round.

The eggs when first laid are surrounded by a single somewhat tough structureless membrane (fig. 1, O.M.).

I have not been able to observe the first stages of segmentation; the earliest which I have to describe is that in which a circular patch of cells has appeared on the egg (fig. 1). The cells have already become rather numerous, so that a diameter of the blastoderm passes through about twenty. The cells (figs. 1 and 2) are of considerable size, and contain very large granular nuclei. Seen from the surface, they appear of much the same size in all parts of the blastoderm; but a section shows that in the central part they are polygonal in shape and more than one layer thick, while towards the circumference they form only a single layer, and at the extreme edge become flattened. Extending from the edges of the blastoderm over the yolk is an exceedingly thin granular layer.

The cells increase in number and decrease in size, the blastoderm spreads more and more over the yolk, and the central thickening, or *Keimstreif*, losing its circular outline, begins to shape itself into the form of the future embryo. In fig. 2A the head end of the embryo is already distinct, and the two frontal lobes (Fr.) have appeared, though as yet there are no traces of appendages. The posterior part of the embryo is still quite indistinct. Whether the blastoderm spreads by the division of the cells of the circular patch described above as in *Oniscus*‡ and *Mysis*, or by the separation of fresh protoplasm from the food-yolk as in *Asellus*,§ I have not been able to determine. The *Keimstreif* becomes more and more elongated, and soon attains the stage shown in fig. 3. In addition to the original membrane, a second very thin one has now appeared, which is for the most part closely applied to the surface of the yolk, but at certain points is slightly separated from it and is easily seen. It is not cellular in structure.

* The kind used for lamps.

† "Gen. organs of Parasitic Isopoda," 'Jour. Anat. and Physiol.,' vol. xi., p. 118.

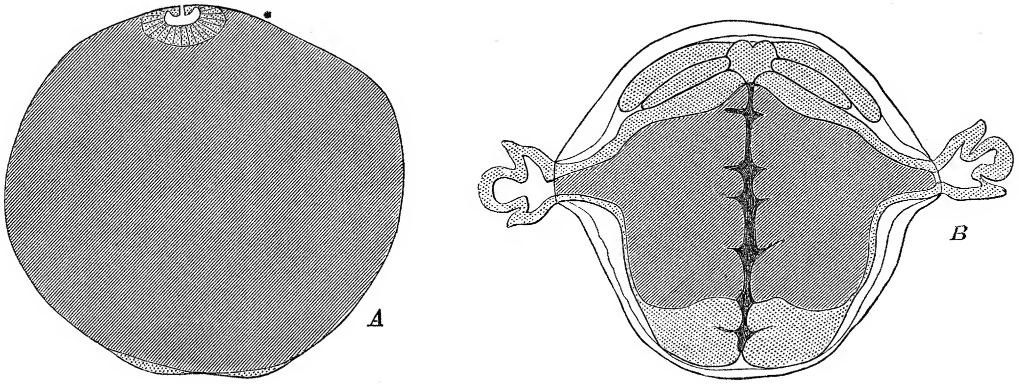
‡ BOBRETZKY, *loc. cit.*

§ VAN BENEDEN, Bull. Acad. Roy. Belg., t. xxviii.

Fig. 3 shows the ventral side of the egg at this stage. The segments of the head and thorax are quite distinct; but in the abdominal region they have not yet become distinguishable. A depression (M) at the anterior end of the embryo is the involution to form the fore-gut; it is very slight, and appears as a dark mark when seen from the surface. Extending from the mouth towards the hinder end of the body in the median line, is a dark mark caused by the surface of this portion of the embryo being lower than the rest. It is along this line that the nervous system will be developed. The ventral half of the egg is covered by a layer of flattened cells extending in all directions from the edges of the *Keimstreif*, and in the hardened egg appears to the naked eye much lighter in colour than the dorsal surface. With the microscope it may be seen that there are cells also on the dorsal surface, but they are very much thinner and less easily seen than those on the ventral surface. On the dorsal surface of the egg at the anterior end is a transversely elongated band of cells (fig. 4, D) connected with the embryo only by means of the flattened dorsal cells. This is the rudiment of a peculiar organ which at a latter period occupies the dorsal part of the first thoracic segment, and which I shall speak of in future as the *dorsal organ.*

It may be well at this point to say a few words about this organ, and the various structures which have been regarded as identical with it in other crustacea. In *Cymothoa* it does not long retain the structure described above, but soon becomes circular, and the cells composing it more columnar. As development proceeds it increases in size, and causes a considerable depression in the yolk; at the same time, a cavity is developed in its interior, of the shape shown in the diagram A (fig. 1, *woodcut*). It is now seen to be in connexion with the inner egg-membrane, though

Fig. 1.




Diagrams showing dorsal organ. A, *Cymothoa;* B, *Asellus.* (VAN BENEDEN, Bull. Acad. Roy. Belg., t. xxviii.)

whether this has been the case all along I am unable to say. Having attained this form, it undergoes no further modification during the period in which I have been able to observe it. Considerably after the embryo had escaped from the egg-

membranes it was still present, and it then showed no signs of atrophy. In the adult, however, I could find no trace of it.

Organs more or less resembling this have been described in many of the Crustacea, and in some other groups of Arthropods. In the Amphipods* it appears to be constantly present, and tolerably uniform in structure. It consists of a circular mass of cells attached to the inner egg-membrane, in which usually a cavity becomes developed. It occupies the same position as in *Cymothoa*, and disappears probably about the same time.

Among the Isopoda it is much more variable. In *Oniscus*† it appears first as a patch of rounded cells on the dorsal surface of the embryo. At a later stage this disappears, and is replaced by a short cellular stalk, from the upper end of which a cellular membrane spreads, like a broad saddle, over the back and sides of the embryo.

In the embryo of *Asellus*‡ the well-known paired leaf-like appendages probably represent the dorsal organ. They arise on each side of the body behind the head as simple oval masses of cells, which soon increase in size and become three-lobed. A cavity is formed in each lobe, which becomes filled with fluid. The three cavities eventually unite, and form a single trilobed cavity open to the yolk, in which free cells and drops of food-yolk are sometimes found. At a certain period these organs attain so great a development that they break through the egg-membranes, and protrude freely on each side of the embryo. Diagram B (fig. 1, *woodcut*), taken from one of VAN BENEDEN's figures, represents these organs in this condition. They occupy nearly the same position as the two ends of the elongated cellular band found in the early stages of *Cymothoa*.

In *Praniza*§ an unpaired dorsal organ is formed in the usual position. It consists of a rounded mass of cells, and is in connexion with the inner egg-membrane, which at an early stage is evidently cellular, especially in front.

Among the other groups of Crustacea, *Cuma*‖ possesses a similar organ.

In *Mysis*¶ a mass of cells appears on each side of the body behind the head, in the same position as the leaf-like appendages of *Asellus*. A hollow appears in each of these masses, which becomes filled with fluid, and apparently communicates with the yolk. They disappear very early. It is very doubtful whether these organs occur in other Podophthalmata.

In the Spiders,** a mass of cells, "cumulus primitif" of CLAPARÈDE, appears very

* MEISSNER, Zeit. für Wiss. Zool., bd. vi.; LA VALETTE, Abhand. der Naturforsch-Gesell. zu Halle, bd. v.; FRITZ MÜLLER, 'Facts for Darwin'; EMIL BESSELS, Jenaische Zeit., bd. v.

† BOBRETZKY, Zeit. für Wiss. Zool., bd. xxiv.

‡ DOHRN, Zeit. für Wiss. Zool., bd. xvii.; E. VAN BENEDEN, Bull. Acad. Roy. Belg., t. xxviii., 1869.

§ DOHRN, Zeit. für Wiss. Zool., bd. xx., 1870.

‖ DOHRN, Jenaische Zeit., bd. v., 1870.

¶ E. VAN BENEDEN, Bull. Acad. Roy. Belg., t. xxviii., 1869.

** CLAPARÈDE, 'Recherche sur l'Evolution des Araignées.'

early on the dorsal surface of the embryo, and was supposed by its discoverer to represent the dorsal organ of the Crustacea.

LEUCKART is stated to have described a similar structure in the Pentastomidæ, but, unfortunately, I have been unable to refer to his paper. Various speculations have been put forward with reference to this organ, the most important of which will be found in two papers by Dr. DOHRN—one in the 'Journal of Anatomy and Physiology,' 2nd series, vol. i., 1868, and the other in the 'Jenaische Zeitschrift für Naturwissenschaft,' bd. v., 1870—and in a paper by M. EMIL BESSELS, 'Jenaische Zeit.,' bd. v., 1870. In the two last papers full references are given to the extensive literature of this organ. A lengthy discussion of these theories would be out of place here, but I may say that they all agree in regarding the dorsal organ, including the leaf-like appendages of *Asellus*, as being rudiments of some ancestral structure, and no longer of any use to their possessors. There is, no doubt, a good deal to be said for this view; and in cases such as *Cuma*, *Praniza*, and more especially the Spiders, where the organ is never large and soon disappears, it may well be regarded as a rudiment. But in the case of *Asellus*, *Oniscus*, and *Cymothoa*, the organ attains a considerable size, and its production must be a great tax on the resources of the egg—so great, indeed, that it is difficult to believe it would have retained such dimensions unless it performed some important function. It seems possible that the great variations in structure which it presents in different animals may be explained by supposing that it is really the remains of some lost structure, and that, in some cases, it is useless and has nearly disappeared, while in others it has been taken advantage of to perform various special functions, and has thus become modified in various ways.

I will now return to the development of *Cymothoa*.

Sections of an embryo at stage II. show that the ventral wall is formed of a single layer of columnar cells, beneath which are a few scattered cells more or less easily distinguishable as a distinct layer. From the columnar epiblast cells will be developed the epidermis, the central nervous system, the eye, and the fore- and hind-guts, together making up practically the whole gut of the adult. From the lower layer of cells the muscles, connective tissue &c., the liver, and a temporary mid-gut (Dottersack) surrounding the yolk, will be developed.

Fig. 5 is a tranverse section through the thorax; in the centre a slight hollow is seen, formed by the lateral parts being somewhat raised above the general level of the surface of the egg. The hollow is the cause of the dark mark running down the ventral line (fig. 3); from the raised lateral portions the limbs will be developed. At the edges of the *Keimstreif* the columnar epiblast cells (Eb.) alter in character rather rapidly, and pass into the flattened cells spreading over the yolk.

At the anterior end of the embryo the epiblast is thickened on each side of the median line, and consists of several layers of cells (fig. 6). It is from these two lateral thickenings that the cerebral ganglia and eyes will be developed. In longitudinal sections (fig. 7) the segmentation of the body is indicated by the epiblast being thrown

into a series of more or less distinct undulations. The lower layer of cells is thicker beneath the centre of each segment than between the segments, but it cannot be said to be distinctly segmented. At the posterior end of the body the cells are less numerous than at the anterior end. Some of these cells are slightly sunk in the yolk and appear to be isolated from the rest, but they may very possibly have been connected with them by means of other cells which lay outside the plane of the section, and which have thus been removed. They are not nuclei, but distinct nucleated *cells*.

On the dorsal surface of the egg, towards the anterior end, the dorsal organ is seen in transverse section (fig. 7D); it consists of a single layer of small cells, thickened in the middle, and causing a slight depression on the surface of the yolk. A series of flattened cells may be seen extending over the surface of the yolk for some distance from both the head and tail ends of the *Keimstreif*, and elongated nuclei occur at various points beyond them.

Though these cells do not appear to form a continuous layer in any one section, yet, after the examination of a number of sections and from the appearance of the entire egg, I have no doubt that they do so in reality.

Their non-appearance as a continuous layer in a single section is probably due to their extreme thinness and to the fact that, like the cells of the dorsal organ, they do not stain nearly so readily as the other cells of the embryo.

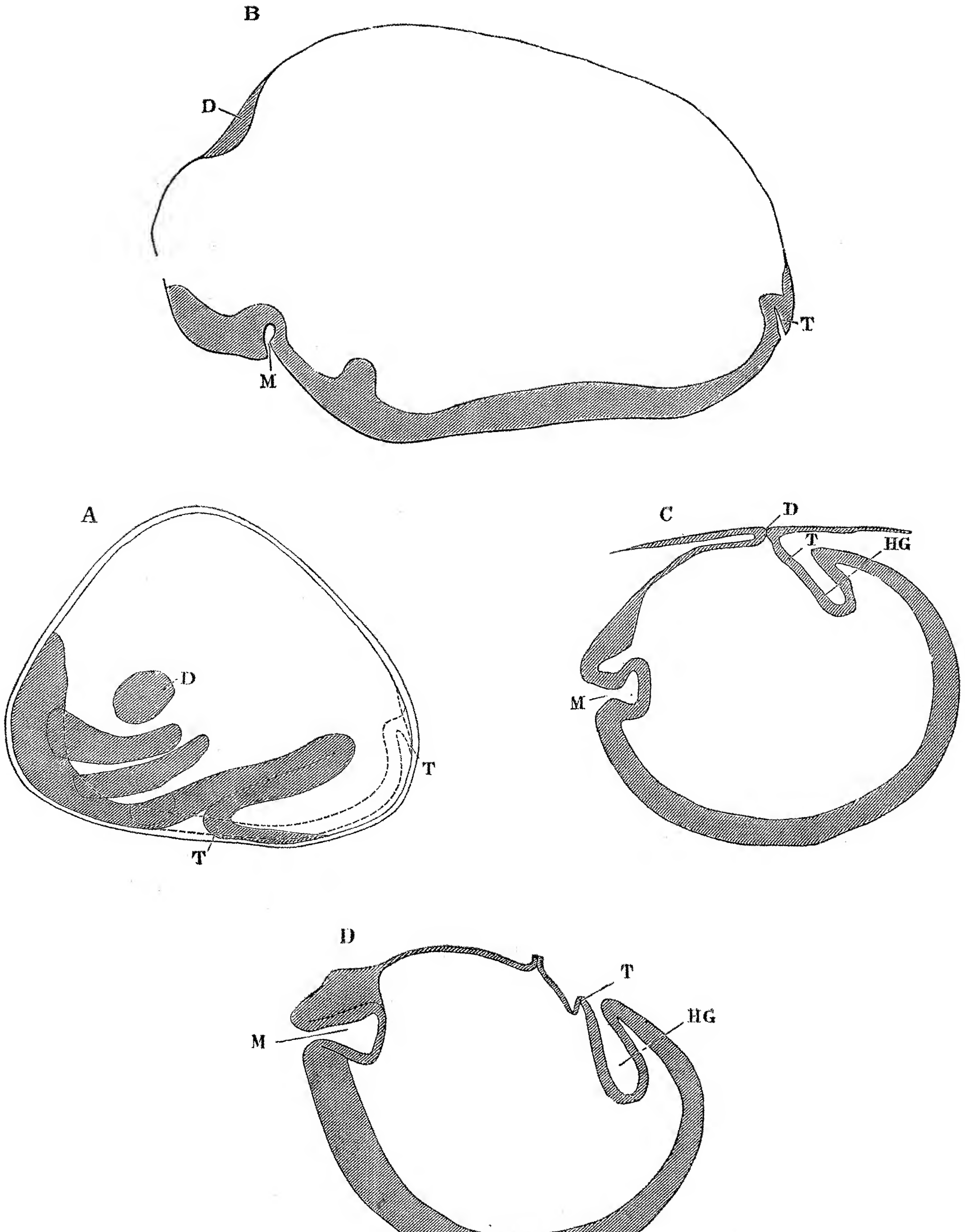
In the next stage the inner membrane has become thicker and is less closely applied to the yolk. All the segments are now quite distinct except the seventh thoracic, which does not make its appearance till a later period.

The direction of the telson (fig. 9, T) should be noticed. It is generally stated that one of the differences between the Amphipoda and Isopoda consists in the direction of the tail of the embyro, which is bent downwards in the Amphipoda and upwards in the Isopoda. Thus FRITZ MÜLLER ('Facts for Darwin,' p. 71) says: "The curvature of the embryo upwards instead of downwards was met with by me, as well as by RATHKE, in *Idothea*, and likewise in *Cassidina*, *Philoscia*, *Tanais*, and the Bopyridæ; indeed, I failed to find it in none of the Isopoda examined by me." And at p. 74: "The Amphipoda are distinguishable at an early period in the egg by the different position of the embryo, the hinder extremity of which is bent downwards." If my figure (fig. 2, B, *woodcut*) is compared with VAN BENEDEN'S* figure of *Mysis*, and with BOBRETZKY'S† figures of *Oniscus*, we shall, I think, be able to see the way in which this difference of bending has come about. In *Mysis* (A), the posterior end of the body is formed very early, and is bent sharply forwards. In *Cymothoa* (B), development proceeds gradually from before backwards, and the posterior end is the last part to appear; it is bent forwards in precisely the same way as in *Mysis*, but naturally forms a smaller protuberance as it here represents but a single segment (the telson), while in *Mysis* it represents several. If the embyro *Mysis* were drawn out as

* "Dévelopment des Mysis," Bull. Acad. Roy. Belg., t. xxviii., 1869.

† Zeit. für Wiss. Zool., bd. xxiv., pl. xxii., figs. 15 and 17.

Fig. 2.




Diagrams illustrating the curvature of the embryo.
A. *Mysis* (Van Beneden, Bull. Acad. Roy. Belg., t. xxviii., 1869). B. *Cymothoa*.
C and D. *Oniscus* (Bobretzky, Zeit. für Wiss. Zool., bd. xxiv.).

indicated by the dotted line it would almost exactly correspond with *Cymothoa,* and this drawing out is what would naturally happen if the development proceeded more gradually from before backwards as in *Cymothoa.* In *Oniscus* (C) the drawing out is completed, the embryo grows almost quite round the egg, and the hind-gut (HG) appears before the telson is formed. When it does appear (D) it is directed dorsally, not on account of any change in its real direction of growth, but because its development has been delayed so long that the embryo has had time to grow nearly round the egg, causing the whole of the posterior ventral surface to point dorsally.

*Cymothoa* may thus be regarded as a connecting link between forms like *Mysis,* in which there is a strong forward bending, and forms like *Oniscus,* in which there is apparently an equally strong backward bending.

The rudiments of the limbs have appeared as small rounded projections, whose free ends point toward the middle line: they are formed of a fold of epiblast, and their central part is filled with a number of cells from the lower layer. Fig. 8 is a transverse section through the thorax; it is slightly oblique, and so does not pass through the point of junction of both the limbs with the body. In the median line between the limbs a thickened mass of epiblast has appeared from which will be developed the ventral nervous system. At this stage it still consists of undifferentiated epiblast cells, and has not become separated from the external or epidermic layer of the epiblast.

The only other point to be noticed in this section is the increase in the number of the cells of the lower layer. Fig. 9 is a longitudinal section slightly to one side of the middle line. At the anterior end the cerebral ganglion is very well marked, and some fibrous tissue has been formed in it. Immediately behind this is the involution to form the mouth and fore-gut; it has increased considerably in size since the last stage. The most interesting feature of this section is the solid rounded mass of lower layer cells (fig. 9, L) situated in the third post-oral segment from which the liver will be developed.

The involution to form the hind-gut has begun, but is less marked than the oral involution. Behind it the telson (fig. 9, T) is very distinct.

The dorsal organ now consists of several layers of cells, and has become circular in shape. In its interior a peculiarly-shaped cavity has made its appearance, and it rather closely resembles one of the "blattformige Anhänge" of *Asellus.*

In the fourth stage the egg has altered somewhat in shape; in the last stage it was a nearly regular oval, but now the head has become more distinct. The positions of the eyes are marked by slight prominences, and the abdominal region has become narrower. The limbs can be distinctly seen through the egg-membranes; they have increased a good deal in size, and are now marked by slight constrictions indicating the positions of the future joints.

Fig. 10 is a transverse section through the anterior part of the thorax. In the middle line between the appendages (fig. 10, Ap.) the ventral nerve cord (N) is

seen. The external layer of epiblast cells has become separated from it everywhere, except at the most ventral point. In the dorsal part of the nervous system two fibrous cords have been formed; these are continuous with the fibrous tissue in the cerebral ganglion. Longitudinal sections show that the ventral nervous system is no longer a continuous mass of cells, but that segmentation has begun at the anterior end and is extending backwards. The bodies marked Ap. are portions of the appendages, which owing to their oblique position have been cut nearly transversely. Their central part consists, as it did in the last stage, of undifferentiated cells. The cells of the lower layer are especially abundant in the neighbourhood of the liver, two of whose cœca are seen on the right and one on the left hand side of the figure. These tubes have been developed from the solid mass of cells seen in the last stage (fig. 9, L).

Their relations to the other parts of the embryo are best seen in a horizontal section, such as that represented in fig. 11. This section passes through the liver on both sides of the animal. Each half of the liver consists of three very short cœcal tubes, opening by a common aperture to the yolk, and, at any rate as far as can be made out from sections, quite unconnected with each other, and with the fore and hind-guts. Between, and a little in front of the liver cœca, the section passes through the top of the fore-gut (FG.) Both the fore- and hind-guts have increased a good deal, and the fore-gut has become dilated at its posterior end to form the stomach.

At the sides of the body the epiblast is folded at each segment, and beneath it are a quantity of still undifferentiated cells, from which the lateral muscles, &c., will be developed. There are also some scattered cells round the liver cœca, and a large number near the fore-gut and cerebral ganglion. The large masses of cells at the anterior end of the section are parts of the cerebral ganglion. The two of these which are in apposition in the middle line, are continuous, on the one hand with the circum-œsophageal cords, and on the other, at a point dorsal to that through which the section passes, with the lateral masses of the cerebral ganglion.

The epiblast covering the sides of the head has become split off from the ganglion, and already at this stage is considerably thickened in the position of the eyes.

Before going on to the next stage it will be best to notice shortly the fate of these two thickenings. I will first describe the structure of the eye in the adult.* Fig. 12 represents somewhat diagrammatically a section passing through the eye transversely to the long axis of the head. Only two divisions of the eye are shown, but as these are all alike they will be enough for the purpose. Beginning with the external surface of the eye, each division is covered by a thickening of the cuticle (C); beneath this comes a transparent, refractive, nearly spherical body (*kristal kegel*), somewhat flattened in front, surrounded by seven large cylindrical pigmented cells (Z). At a short distance beneath the *kristal kegel* these cells are marked by

* For an account of the structure of the eye in the different groups of the Arthropoda, see "Untersuchungen über das Arthropoden-Auge," Dr. H. Grenacher, 'Klinische Monatsblätter für Augenheilkunde.' Mai-heft xv. Jahrgang. Rostock, 1877.

a constriction, and appear to pass through the pigmented membrane (Mbn.) which is parallel to the external surface of the eye. Extending from this membrane to the cuticle, and separating the different divisions of the eye from each other, are a number of pigmented connective tissue partitions (C.T.). These parts are shown in transverse section—that is, in a section made parallel to the surface of the eye—in fig. 13, which represents a single complete division and parts of the partitions (C.T.) dividing it from the six adjacent divisions. The circle (X) marks the position of the *kristal kegel* as it would be seen if the focus were adjusted to a point slightly above the level of the paper. Below this are the seven cells (Z) arranged so as to radiate like the spokes of a wheel from the centre of the *kristal kegel;* each cell at its inner edge contains a small transparent unpigmented body (*Sehstäbchen*).

Following these cells (fig. 14, Z) towards the brain they pass through the membrane (Mbn.), run on separately for a certain distance, and then all coming into close contact, become again constricted and pass into a fine bundle of nerves (figs. 12 and 14, Z″) which soon becomes lost in the fibrous tract marked Op. T. (fig. 14).

All the parts of the eye external to the membrane (Mbn.) are developed from the epiblastic thickenings. Whether the parts internal to this, marked Z′ and Z″, are developments from the epiblast, from the cerebral ganglion, or from both, I have not been able to determine.

In the fifth stage the external appearance is much the same as before; the head and abdomen are a little more distinct, and the limbs have increased in size, the antennæ now covering the mouth appendages. A little pigment has appeared at the posterior border of the eyes.

The segmentation of the ventral nervous system is now complete, and there are sixteen distinct ganglia; these are well shown in fig. 15: a longitudinal section. The two fibrous cords extend to the posterior end of the nervous system, and the skin is now entirely separated from the ganglia.

The mouth and œsophagus are very narrow; the stomach has become larger, and two projections have appeared in its floor.

The hind-gut extends forwards as far as the anterior edge of the fourteenth ventral ganglion. Its anterior end is still closed.

The liver cœca are a great deal larger than in the last stage, and have come into contact with the fore-gut.

Above the hind-gut, and extending beyond it in front as far as the tenth post oral ganglion, and therefore occupying the same position as in the adult, is the heart. Its walls consist of elongated nucleated cells. From its anterior end a band of cells passes forwards to the dorsal surface of the embryo, and from about the middle of its ventral surface another band passes to the anterior end of the hind-gut. Posteriorly it is attached to the dorsum and to the anterior ventral wall of the telson.

The dorsal organ has enlarged a little, but otherwise remains the same as in the third stage.

The formation of the muscles has begun in the abdomen and limbs, the cells being arranged in rows.

*The sixth stage* I have taken is that in which the egg-membranes burst, so that some of the embryos are still in the egg, while others are free.

In the living embryo (fig. 16) most of the organs can be more or less distinctly seen. In the abdominal region the heart (fig. 16, H) is very conspicuous and beats vigorously.

The blood enters it by four valvular openings (V) arranged in a spiral, and leaves it by five anterior aortæ, each of which is provided with valves.

The blood corpuscles are not very numerous, but there are enough to show the course of the circulation, and in those individuals which have escaped from the egg, they can be seen passing through the branchiæ.

Round the edge of each branchial plate, between the two chitinous laminæ of which it is composed, there is a clear space answering the purpose of the afferent and efferent vessels of the organ. The central part of the lamella is occupied by a number of cells, leaving a meshwork of spaces between them.

The blood flows up the inner edge of the lamella, and passes across to the outer edge to return to the heart.

The passage of the corpuscles to and from the gill is very rapid, but they often get entangled in going from one side to the other and remain in the gill for some time.

Occupying the greater part of each side of the thorax are the liver cœca (fig. 16, L). They are of a different colour from the yolk and are filled with a fluid in which are suspended numerous oil drops. These are kept in constant motion by the contractions of the cœca, and sometimes pass from one cœcum to another; the cœca lie entirely above the yolk, and by gently moving the cover-glass can be made to glide about over it without in any way injuring the embryo.

In the second segment behind the head the liver cœca are attached to the fore-gut. The arrangement of these parts cannot be made out in the living state, but by cutting the embryo in half so as to allow the yolk to escape without injuring the liver cœca, it is possible to see the duct, and by gently pressing the cover-glass one can make the oil drops pass from the liver into the fore-gut. Fig. 17 is an optical section of these parts. Two projections bearing hairs may be seen in the front part of the stomach.

The hind-gut can be traced from beneath the heart, in the abdomen, to its junction with the fore-gut, although from its transparency it is not at first very easily seen. Like the liver, it lies entirely above the yolk. For the greater part of its course it is very narrow, but at the anterior end it appears to dilate a little before joining the fore-gut; its walls at this point are extremely thin. At a rather later stage, when the yolk has decreased to about half its present size, it is quite easy to tease out the embryo, so as to see the junction of the fore- and hind-guts and liver cœca.

The yolk at this stage is surrounded by a membrane (Dottersack) continuous with

the point of junction of the fore- and hind-guts. Fig. 18 shows the yolk, liver cœca, and fore-gut teased out in the fresh state; the hind-gut, owing to its extreme tenderness, has been broken off. The yolk-membrane is very thin, and bursts so as to let the yolk rush out on very slight pressure. Its presence is most easily demonstrated by cutting off the abdomen close to its junction with the thorax, and then allowing the cover-glass to press very gently on the embryo. This causes the yolk to protrude from the cut end, and its outline may be seen to be quite smooth and sharp; the least extra pressure at once causes the membrane to burst, and the yolk then immediately streams out. With care, the whole yolk-sac may be dissected out still attached to the fore-gut, as in fig. 18.

In the process of hardening, the yolk-membrane always breaks, and thus allows the yolk to escape into the body cavity, and to occupy positions in which it is not found in the living animal. For this reason sections are not entirely trustworthy, the hind-gut and liver cœca often appearing embedded in the yolk, whereas in the living embryo they are quite free from it. The yolk-membrane cannot in any one section be traced the whole way round the yolk; but in those places where it is supported, such as on each side of the nerve-cord and between the liver cœca, the membrane can be seen in almost every section. There seem to be elongated nuclei here and there in it.

I think there can be no doubt that the yolk-membrane and the cells forming the liver are to be regarded as the hypoblast or lining of the mid-gut, for the liver is only a diverticulum from that organ.

It appeared in an earlier stage (stage III.) that the liver arose from a mass of cells on each side of the embryo, and apparently had no connexion with the rest of the digestive system.

This mode of development is perfectly explained if the yolk-membrane is regarded as the mid-gut. Though its presence cannot be demonstrated in the earlier stages, it no doubt really exists in them; and it would probably not be wrong to trace it back to some of the lower layer cells in the second stage, from which the liver (stage III.) arose, or even perhaps to the lower cells in the first stage. It is thus probable that the liver does not arise, as at first sight might appear, from two isolated masses of cells, but in the normal way by a prolongation of the cavity of the mid-gut.

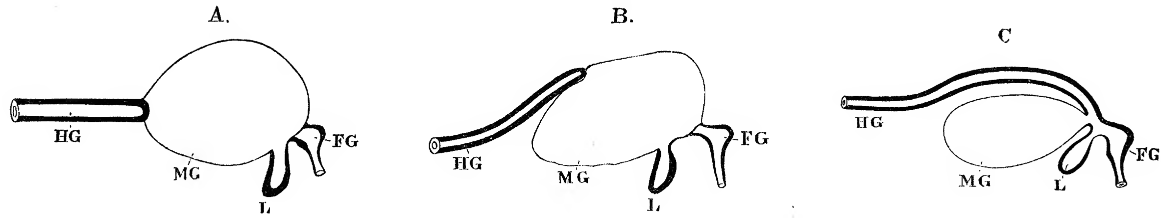
The arrangement of the parts becomes clear on remembering the large quantity of food-yolk in the egg.* It may be supposed that, owing to the growth of the hind-gut being more rapid than the absorption of the food-yolk, the point of junction of the hind- and mid-guts gets carried more and more forward (see diagrams A, B, C, fig. 3, *woodcut*) along the dorsal surface of the yolk until at last it reaches the fore-gut, into which the hind-gut opens, the mid-gut remaining as a sac enclosing the yolk, and opening at the junction of the fore- and hind-guts.

As the yolk disappears the mid-gut disappears with it, and the alimentary canal

* More than in any other Crustacean except *Astacus* (?).

of the adult consists practically of the fore- and hind-guts alone, the liver being the only permanent representative of the hypoblast. The mid-gut in these animals is therefore only a temporary structure. That this interpretation of the facts is the true

Fig. 3.

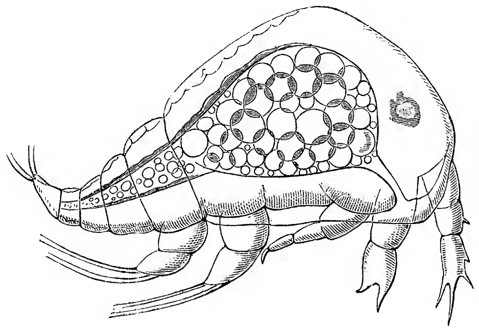



Diagrams illustrating successive stages in the development of the alimentary canal.
HG. Hind-gut. MG. Mid-gut. FG. Fore-gut. L. Liver.

one, is rendered more probable by the fact that among certain other Crustacea the mid-gut is formed from the yolk-membrane.

Fig. 4 (*woodcut*), copied from VAN BENEDEN's paper on *Hessia colorata*,* shows this very clearly, and corresponds almost exactly with the woodcut, fig. 3, A. VAN BENEDEN does not give a detailed account of the mode of development of these parts, but mentions incidentally that the mouth and œsophagus are formed by involution. He thus describes the figure: "L'œsophage relie la base de la trompe buccale à l'élargissement considérable du tube digestif (yolk-membrane) qui renferme les restes

Fig. 4.



*Hessia colorata* (VAN BENEDEN, Bull. Acad. Roy. Belg., t. xxix., 1870, pl. xxix., fig. 15).

du vitellus ; il s'est considérablement allongé, et l'on distingue facilement ses parois. On peut suivre le tube digestif dans toute sa longueur : fortement renflé en avant, il se rétrécit progressivement en arrier (hind-gut) pour s'ouvrir à l'extrémité postérieure de l'abdomen entre les deux appendices caudaux. Il renferme le reste de la masse deutoplasmatique qui a singulièrement diminué dans le cours du développement embryonnaire, ayant été employée à former successivement les différents organes de l'embryon."

* Bull. Acad. Roy. Belg., t. xxix., 1870, pl. xxix., fig. 15.

The same mode of development occurs probably in *Cuma, Praniza, Portunus,** &c. In his account of the development of *Asellus aquaticus*, Dr. DOHRN† goes rather fully into the question of the meaning of the yolk-membrane (Dottersack). After describing his observations on the development of the digestive organs, which appear to agree in all essential points with what I have found in *Cymothoa*, he says:—"Ueber das Verhältniss der Entstehung der Leberschläuche—denn durch Auswachsen des hinteren Endes nehmen diese Organe bald die Schlauchform an—zum Dottersack habe ich nur Vermuthungen. Möglich ist es, dass der Dottersack schon vor der Bildung der Leberwandungen besteht, dass letztere also Ausstülpulgen desselben würden. Wahrscheinlich ist mir indess dass Gegentheil, und dass der Dottersack sich um die innere Oeffnung des Leberschlauches herumlegt. Diese Bildung allein lässt uns aber schon die Möglichkeit einsehen, dass die Abscheidung des Dottersacks kein so allgemeiner Vorgang ist, als es haüfig aufgefasst wird. Gewiss stehen keine theoretischen Bedenken der gleichzeitigen und allgemeinen Umhüllung des Dotters durch den Dottersack in den Fällen entgegen, wo seine Wandung sich zum Mitteldarm umwandelt und wo alle accessorischen Gebilde des Darmcanals durch Ausstülpungen entstehen. Und wenn man die directe Beobachtung für diesen Vorgang ins Feld führen kann, so muss ja jegliches auf abweichenden Untersuchungen in analogen Fällen basirtes Urtheil seine Beweiskraft verlieren. Aber ich glaube, es würde irrthümlich sein, den Analogieschluss von derartig festgestellten Entwicklungs- und Bildungsweisen nun auf die übrigen noch zweifelhaften Fälle anzuwenden, und meine bisherigen Untersuchungen lassen mich durchaus bezweifeln, dass bei *Asellus aquaticus* ein Dottersack ensteht, der an allen Puncten gleichzeitig den Dotter umhüllt. Leider bin ich trotz tagelanger und häufig wiederholter Beobachtungen nicht im Stande, ein sicheres Resultat über die, wie es scheint, sehr verwickelten Verhältnisse zu bieten; ich kann nur angeben, was ich gesehen und was ich daraus schliesse, ohne mehr für meine angaben in Anspruch zu nehmen, als dass sie wahrscheinlich seien."

I think there can be no doubt that fig. 18 proves that the yolk is completely surrounded at one time by the yolk-membrane, and it may therefore be fairly assumed that the same is the case in *Asellus*, although Dr. DOHRN did not absolutely succeed in demonstrating it.

In *Oniscus*,‡ according to BOBRETZKY'S very clear description, the mode of development is somewhat different, although it results in the formation of a digestive tract having the same homologies as that of *Cymothoa*.

The first step in the development of the egg is the separation of the formative yolk from the food-yolk. The former then segments and a single layer of cells is formed which spreads gradually over the surface of the egg. Before the yolk has

* DOHRN, "Untersuchungen Ueber Bau und Entwick. der Crustacean," Jenaische Zeit., bd. v., 1870, and Zeit. für Wiss. Zool., bd. xx., 1870.

† DOHRN, "Asellus," Zeit. für Wiss. Zool., bd. xvii., 1867.

‡ BOBRETZKY, Zeit. für Wiss. Zool., bd. xxiv., 1874.

been completely surrounded a second layer of cells has made its appearance under the central part of the blastoderm. These cells rapidly increase, and at the same time sink into, and become filled with the yolk. Meanwhile the blastoderm has surrounded the egg, the *Keimstreif* has been formed, and the involutions for the fore- and hind-guts have appeared. The hypoblast cells now begin to separate themselves again from the yolk, and gradually become arranged so as to form the wall of the liver, which, from the first, surrounds a considerable portion of the yolk. There is no yolk-membrane. The hind-gut grows forwards and becomes connected with the liver, in which the whole of the yolk is now contained, and eventually unites with the fore-gut.

The following seems to me to be the most satisfactory explanation of the differences in the development of the hypoblastic organs in *Cymothoa* and *Oniscus*. On comparing the yolk-membrane of *Cymothoa* with the mid-gut of *Hessia* (fig. 4, *woodcut*), it appears that a degeneration has taken place. In *Hessia* there is a distinctly cellular and functional mid-gut, while in *Cymothoa* it is extremely thin and disappears entirely in the adult. In *Oniscus* it has completely disappeared, and at the same time the mode of development of the liver has become altered to enable it to perform to a certain extent the function of the yolk-membrane in enclosing the yolk. Instead of arising as in *Cymothoa* (fig. 9) from a solid mass of hypoblast cells which penetrates into the yolk only to a small extent, and then gradually becomes hollowed, the liver is formed from hypoblast cells, which, at an earlier period, penetrate much more deeply into the yolk, and arrange themselves in such a way that, from the first, they surround a large portion of the yolk, and very soon completely enclose it. We must therefore regard the penetration of the hypoblast cells into the yolk in *Oniscus* as in no way connected with a primitive invagination or gastrula, but as a modification of the mode of formation of the liver and mid-gut found in *Cymothoa*.

In *Astacus** the case appears different, and until we have a more complete history of its development, probably no comparison of any real value can be made between it and *Cymothoa*.

Fig. 19 is a transverse section through the thorax of an embryo, of the same stage as fig. 16. The hind-gut (HG) is a very narrow tube, with scarcely any lumen. On each side of it are the three liver cœca (L); their walls are very thin, the cells forming them scarcely seeming to be in contact. The muscles in the sides of the body and limbs are now distinctly striated.

The dorsal organ (fig. 16) is still of the same form, and contains the same peculiarly shaped hollow.

After their escape from the egg, the embryos remain in the brood-pouch of the mother until the whole of the yolk is absorbed. When they leave her they are very active, and swim well. Fig. 21 represents one of these young. It was one of a brood which I succeeded in bringing up by keeping the fish, in whose mouth the mother

* REICHENBACH, Zeit. für Wiss. Zool., bd. xxix., 1877; BOBRETZKY, *Astacus*.

lived, in a glass covered with a piece of gauze to prevent the escape of the young. They all, however, succeeded in escaping except three. When these first came out their livers were filled with oil-drops. I kept them and examined them every day with the microscope. There was less oil each day, and they got more and more transparent. For several days I could not get any proper fish to put them on, and the oil had so much diminished that they had only one or two small drops left in their livers, and must have been very hungry, for directly I put them on the fish they stuck in their claws and held on tight. It is worthy of notice that, although embryos of a species which lives in the mouth, they began by fixing themselves on the outside of the fish, where they seemed quite happy. I was unfortunately unable to trace their development further, as the fish on which they were placed died in the night, and in the morning when I found them the embryos were dead. Although before they fixed themselves to the fish they were so transparent that all the organs could be easily seen, I was unable to make out any trace of either the generative organs or of the so-called renal tubules.

It seems probable that these organs may be developed at the time that the limbs ot the seventh thoracic segment appear, since they are both connected with it.

## Description of the Figures.

The same letters are used in all the figures.

Ab. Abdomen.
An. Antenna.
Ap. Appendages.
C. Thickened cuticle forming cornea.
C.G. Cerebral ganglion.
C.T. Connective tissue.
D. Dorsal organ.
E. Eye.
Eb. Epiblast.
FG. Fore-gut.
FG′. Gullet.
FG″. Stomach.
Fr. Frontal lobes.
H. Heart.
HG. Hind-gut.
I.M. Inner Membrane.
L. Liver.
L.D. Duct of liver.
M. Mouth.
Mb. Cells beneath the epiblast.
Mbn. Pigmented membrane.
Ms′. Muscles.
N. Nervous system.
O.M. Outer membrane.
Op.T. Optic tract.
T. Telson.
Th. Thorax.
V. Valves of heart.
X. *Kristal kegel.*
Y. Yolk.
Z.Z′.Z″. Sensory parts of eye.

Fig. 1. Whole egg, Stage I. From a hardened example.
Fig. 2. Section through centre of blastoderm, Stage I.
Fig. 2A. A little later than the last. From a hardened egg.
Fig. 3. Whole egg, Stage II. Ventral side. From a hardened egg.
Fig. 4. The same ; dorsal surface.
Fig. 5. Transverse section through thorax of the same.
Fig. 6. Transverse section through frontal lobes of the same.
Fig. 7. Longitudinal section of the same not quite in the middle line.
Fig. 8. Transverse section, Stage III.
Fig. 9. Longitudinal section of the same, a little to one side of the middle line.
Fig. 10. Transverse section, Stage IV.
Fig. 11. Horizontal section, same stage.
Fig. 12. Longitudinal section of the eye (transverse of head): adult.
Fig. 13. Horizontal section of the eye (longitudinal of head): adult.
Fig. 14. Transvere section of head: adult.
Fig. 15. Longitudinal section in median line, Stage V.
Fig. 16. Whole embryo alive, Stage VI.
Fig. 17. Optical section of junction of liver cœca and fore-gut, fresh state, same stage.
Fig. 18. Yolk enclosed in its membrane and liver cœca teased out in the fresh state, same stage.
Fig. 19. Transverse section through thorax, same stage.
Fig. 20 and 21. Embryos as they leave their parent.

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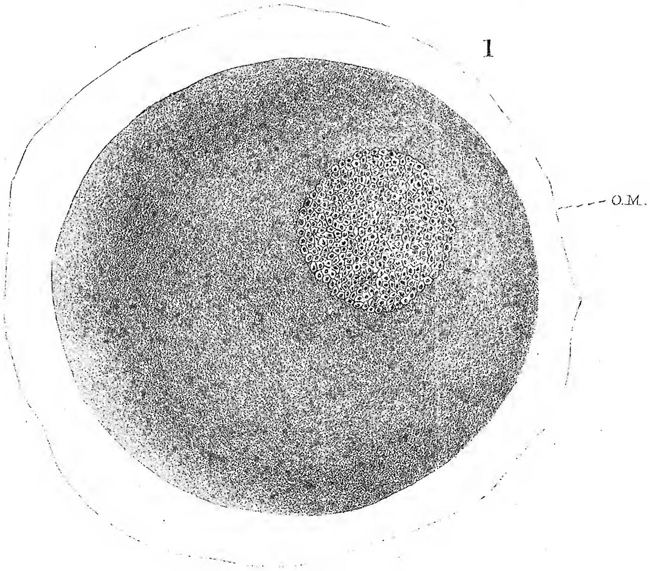


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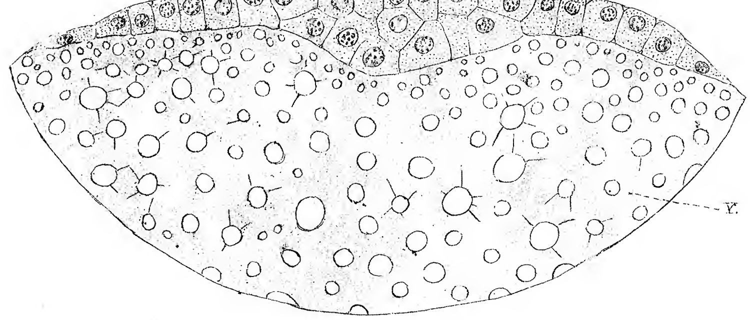


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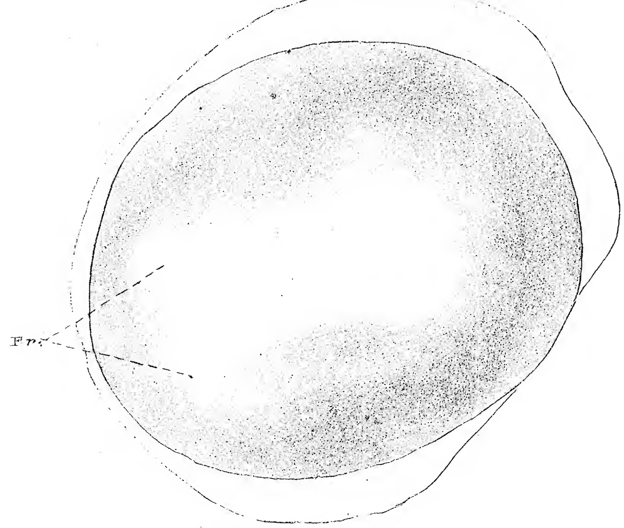


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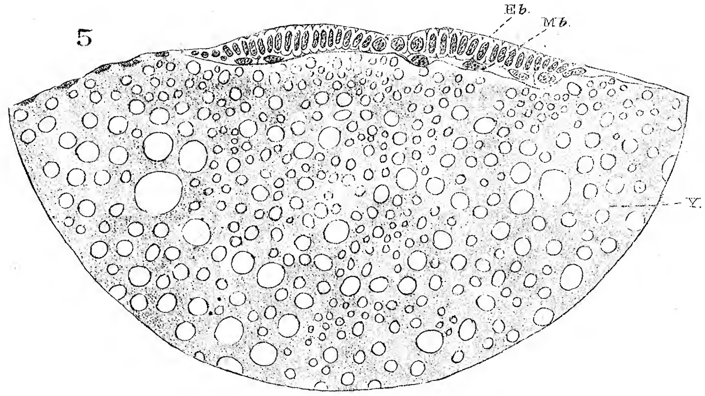


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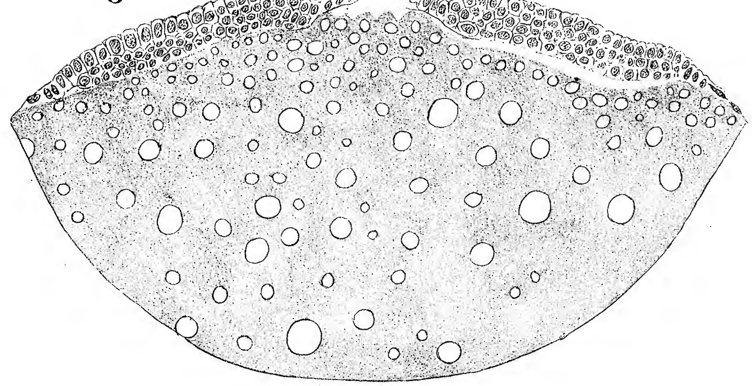

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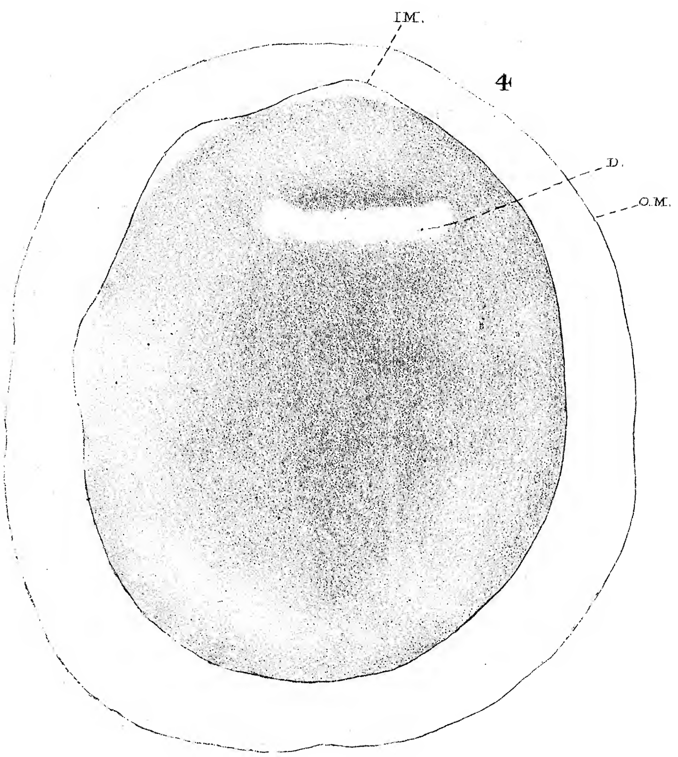


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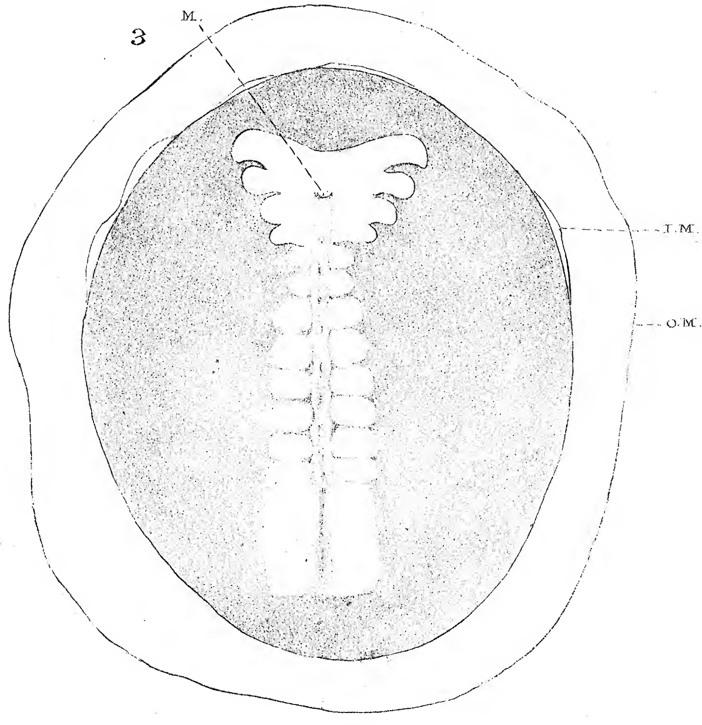

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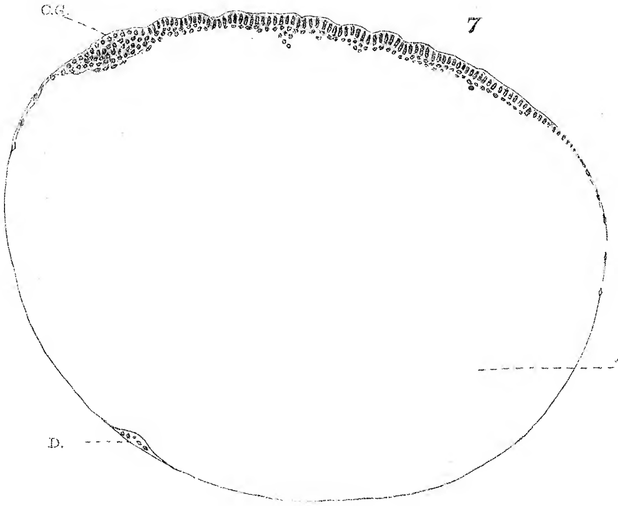


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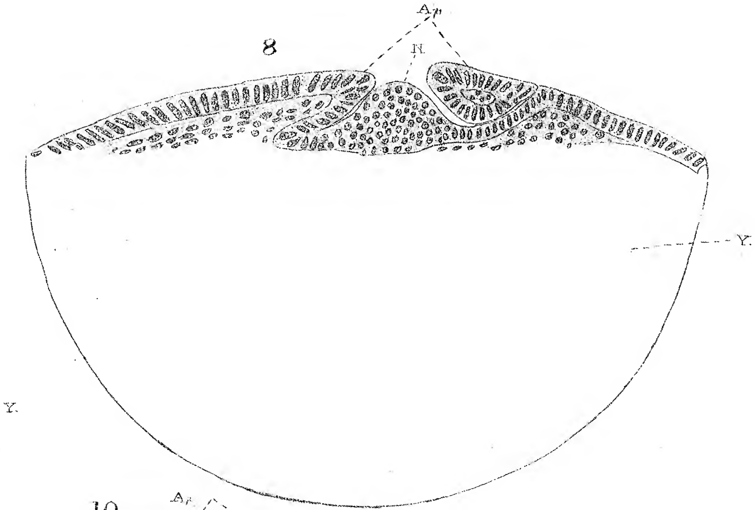


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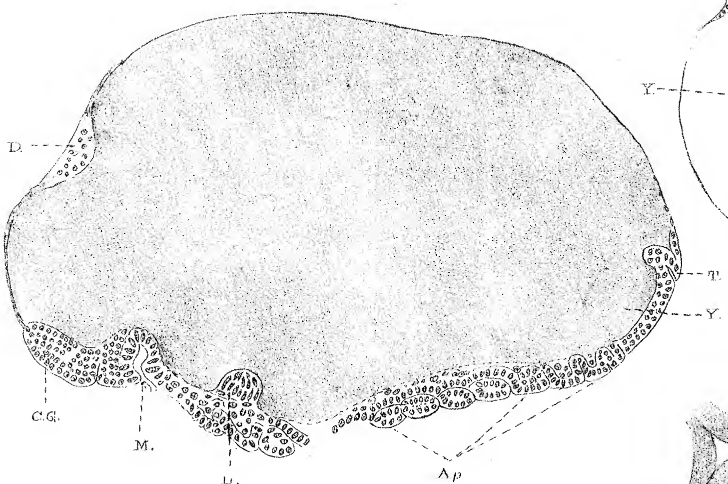


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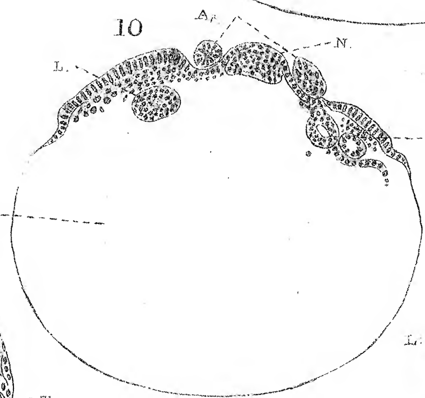


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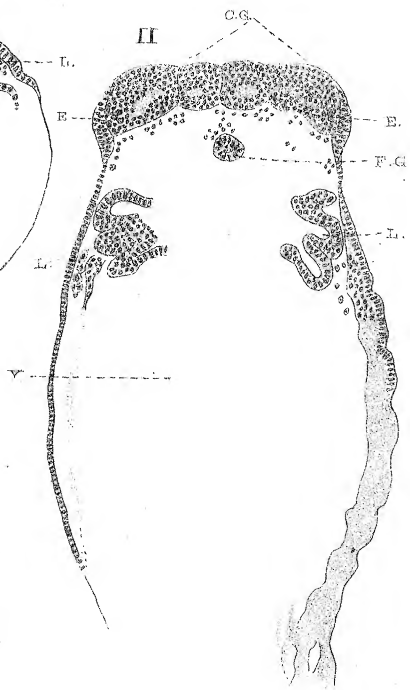


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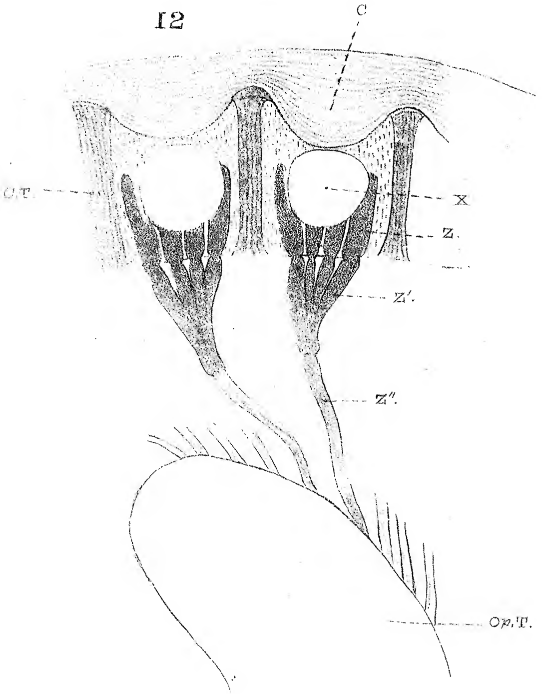


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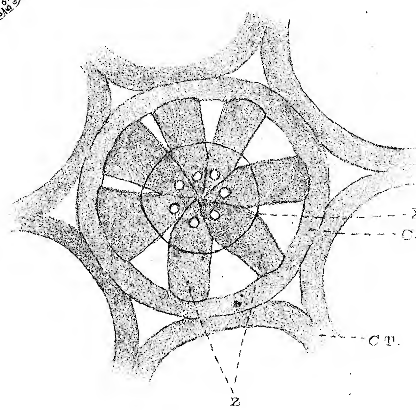


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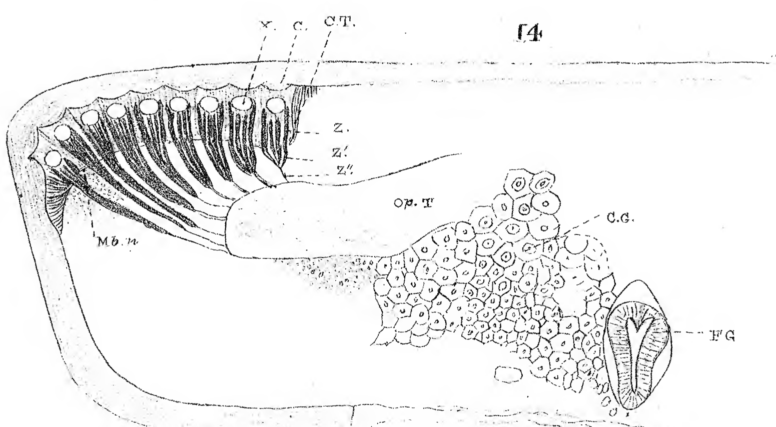


West, Newman & Co. lith.

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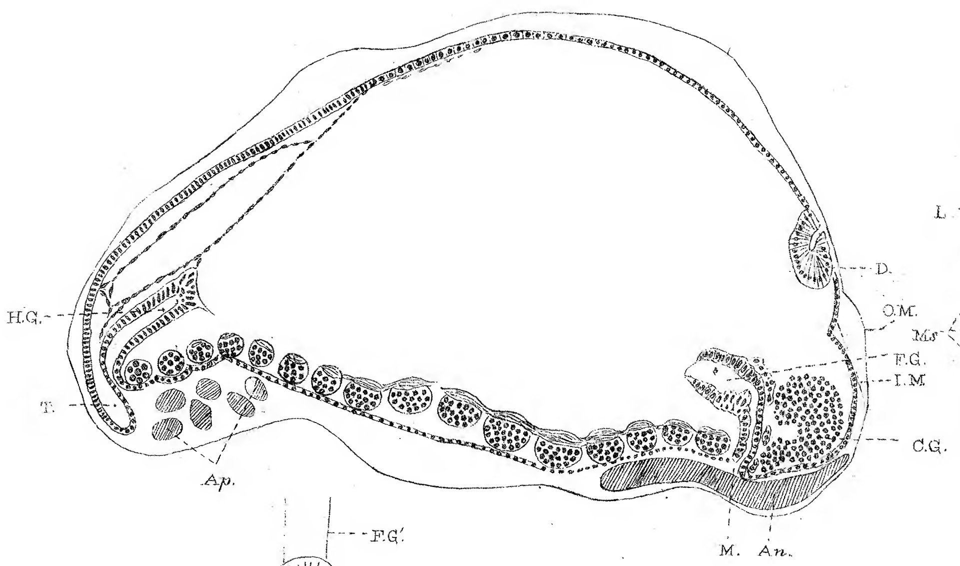


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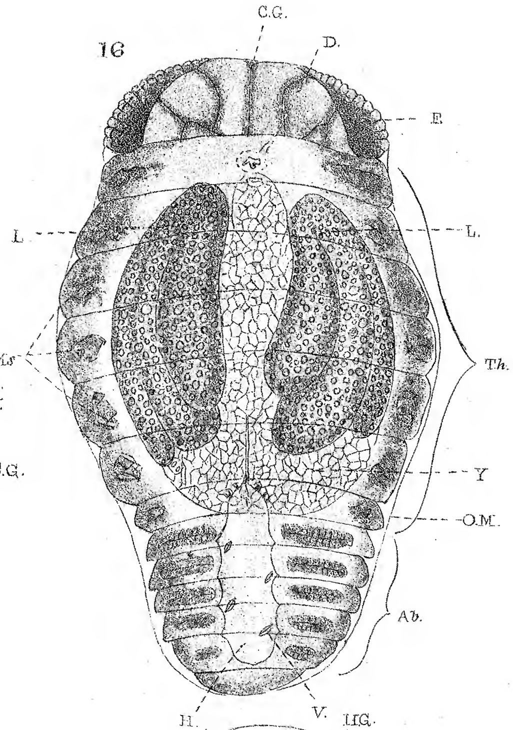


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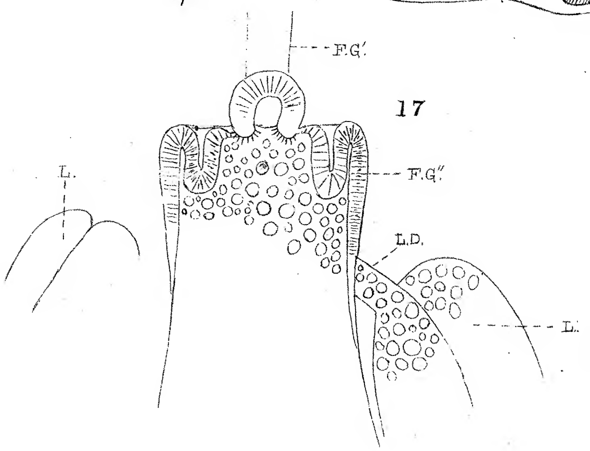


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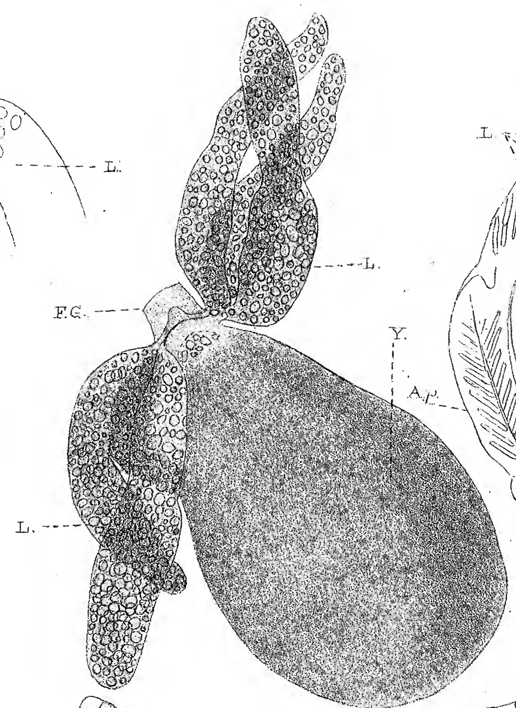


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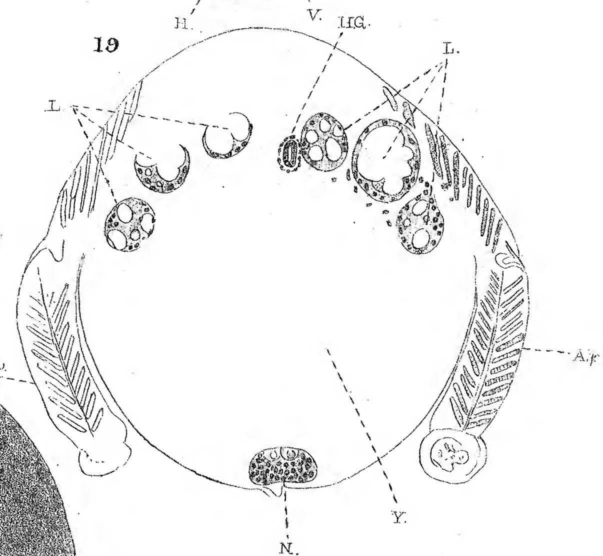


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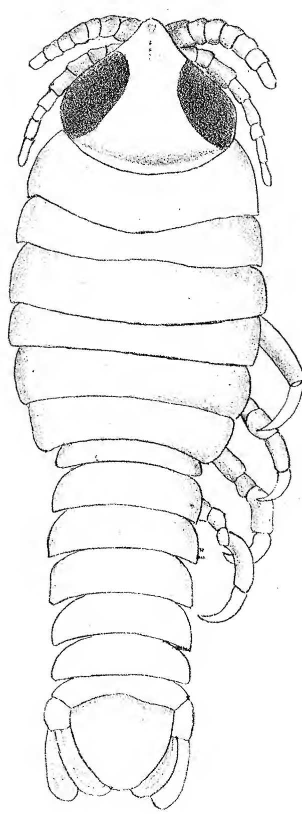

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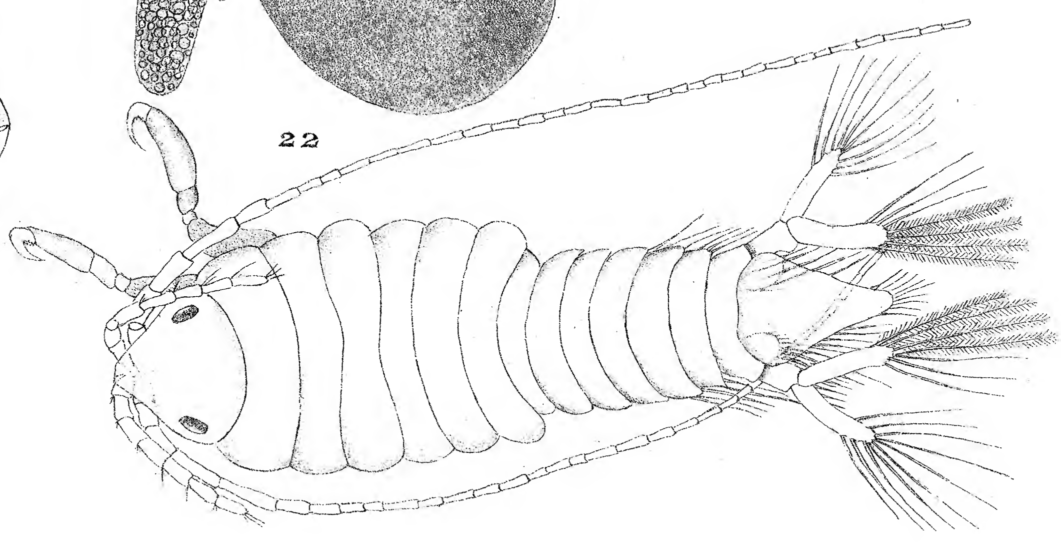

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